LITTER DECOMPOSITION IN A COOL TEMPERATE WOODLAND

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I. INTRODUCTION

The aim of this paper is to present some data on leaf litter decomposition and nutrient change in leaf litter during the initial stages of decomposition (i.e., 0-18 months following leaf fall). The study was undertaken in a deciduous woodland (with *Populus tremuloides* Michx. and *P. balsamifera* L. as the dominant tree species) exposed to extremes in climatic conditions. This general decomposition study was carried out as part of an integrated investigation of the roles of various groups of litter and soil inhabiting organisms in decomposition processes and of the interactions between such groups of organisms. Some data on these organisms have already been published (DASH, 1970 ; DASH and CRAGG, 1972a, b ; PARKINSON, 1971 ; MITCHELL, 1973 ; CARTER and LOUSIER, 1973 ; LOUSIER, 1974).

The study reported here is comparable with many, as yet unpublished investigations carried out as part of the International Biological Program (section PT), and with the studies reported by van CLEVE (1971), van CLEVE and SPRAGUE (1971), ANDERSON (1973a, b), GOSZ et al. (1973) and LEMEE and BICHAUT (1973). During this present investigation, problems of methodology in decomposition studies similar to those discussed by ANDERSON (1973a) were encountered and will be discussed in this present contribution.

Site Description

The study site was a cool, temperate aspen woodland at 1400 m in the front range of the Rocky Mountains, Alberta, Canada (51°21'N, 115°2'W). The woodland was on a well drained south-facing slope. The climate of the region is essentially continental, characterized by short, dry summers and relatively long, cold winters with intermittent warm chinook winds.

The soil has been classified in the orthic grey luvisol sub-group, and has a surface organic horizon easily separated into L, F and H layers. The soil is frozen from mid-November to mid-April and has a continuous snow cover from mid-December to mid-April. Soil moisture is near or above field capacity during the period of snow melt and heavy precipitation (spring and early summer), but from mid-July to

mid-September it declines almost to the permanent wilting point. Data on various meteorological conditions for the site are summarized in Figs. 1 and 2.

The tree layer of vegetation is dominated by *Populus tremuloides* with *Populus balsamifera* being less frequent in occurrence. The understory was composed mainly of various grasses and herbs. More details on the soil and vegetation of the area have been given by PARKINSON (1971) and LOUSIER (1974).

Leaf fall occurred over a period of approximately two weeks in the latter half of September, and a summary of the data obtained on above-ground litter imput for the study site is given in Table 1.

II. METHODS

Leaves of *P. tremuloides* and *P. balsamifera* were caught in above-ground nets, air-dried, enclosed in litter bags and placed in field plots at the study site. The litter bags were of 3 mm nylon mesh, 20 cm x 20 cm in size. 100 bags each of *P. tremuloides* (10.50 ± 0.35 g bag^{-1}) and *P. balsamifera* (5.89 ± 0.30 bag^{-1}) were placed in the field plots after being air-dried (21°C for 3 weeks). The difference in weight of leaves of the two tree species was necessitated by the difference in leaf size of the species - to use 10 g of leaves of *P. balsamifera* would have required litter bags nearly twice as large as those used for *P. tremuloides*.

From each type of litter, 20 bags containing litter were taken at random and oven dried at 80°C for 48 h and the oven-dry weight correction factor determined. Litter moisture contents were 6.95 ± 0.35 % and 8.23 ± 0.60 % for *P. tremuloides* and *P. balsamifera* respectively.

The litter bags were placed amongst the freshly fallen litter in the field plot approximately one month after leaf fall and 10 bags of each litter type were sampled at the following intervals after burial in the field :

1 month :	soil frozen, light snow cover, late fall
5 months :	soil thawed, snowfree, early spring
8 months :	early summer
12 months :	mid fall
18 months :	early spring

At each sampling time the sampled bags were returned to the laboratory, extraneous material was removed, the wet weight of the leaf material was measured, and following this the material was oven-dried at 80°C for 48 h and the oven dry weight was measured.
The replicate oven-dried samples of each species were then combined and analyzed for a number of elements of which quantitative data are presented here for C, N, Ca, Mg, K and P.

III. RESULTS

1) Dry weight loss :

The loss of dry weight in leaf litter of the two *Populus* species over an 18-month period is shown in Table 2 and Fig. 3. During this 18-month period, the dry weight loss in *P. tremuloides* litter was significantly greater ($P < 0.05$) than that for *P. balsamifera*. Apparently the largest weight loss occurred over the period covering fall freezing, winter, and spring thawing.

OLSEN (1963) described equations for expressing rates of decay under varying situations. Confining litter in litter bags and measuring differential increases in weight loss is a special case of decay with no production (i.e:, litter input into decay system = 0). The equation for this situation is $X/X_0 = e^{-kt}$, where X/X_0 is the fraction of weight remaining at time t, e is the base of natural logarithms, and k is the decomposition constant. The k values for *P. tremuloides* and *P. balsamifera* are given in Table 2. The expression of dry weight loss as a negative exponential function permits the calculation of litter "half-life" (0.693/k) and the time required for loss of 99 % dry weight (5/k). The half-life and 99 % decomposition time values are 2.4 and 17.7 years for *P. tremuloides* and 3.3 and 23.6 years for *P. balsamifera*.

2) Nutrient Change

The nutrient change data are summarized in Tables 3 and 4. Nitrogen concentrations (Table 3) and the absolute weight of nitrogen per litter samples (Fig. 4) increased and the C:N values were generally lower for *P. tremuloides* than for *P. balsamifera*, except for the data obtained 12 months after burial of the litter bags when a 30 % increase in nitrogen content in balsam and a 7 % decrease in nitrogen content in aspen were recorded.

The percent carbon and hydrogen contents of the leaf litter of the two *Populus* species showed changes of generally less than 1 % throughout the study period, indicating carbohydrate loss to be directly proportional to dry weight loss. The concentrations of calcium, magnesium and phosphorus were similar for both leaf litter of *P. tremuloides* and *P. balsamifera*, while potassium concentration was about 50% lower in *P. tremuloides*.

Changes in concentration with time of four macronutrient elements are presented in Table 4. Concentrations of calcium and magnesium increased by 30 % and 12-25 % respectively over the study period, while potassium levels decreased 40-65 % during the same period. Phosphorus concentrations showed a slight decline over 12 months ; however fluctuations in phosphorus concentration were recorded during this period - increasing during the spring burst of decomposer activity and declining (stabilizing ?) during the summer.

Calcium levels in the litter held in litter bags after 12 months were equivalent to the levels recorded in the A_0F layer. Potassium levels were the same as those recorded for the A_0L. Magnesium and phosphorus levels were higher in litter in litter bags than in any layer of the organic horizon but most closely approximated to levels in the A_0F and A_0H layers.

IV. DISCUSSION

The data on rates of decomposition of leaf litter of *P. tremuloides* and *P. balsamifera* in comparison with similar data for decomposition of leaf litter material of a range of deciduous tree species are given in Table 5. This demonstrates, even taking into account the data from Alaska, a generally much lower decomposition rate in the *Populus* site under present study. However, in comparison with various tundra sites, there is a higher rate of decomposition of *Populus* leaf litter. Differences recorded between decomposition rates of *P. tremuloides* and *P. balsamifera* under the same environmental conditions may be ascribed to differences in substrate quality between these two species, however little work has been done, as yet, on this aspect.

The use of the negative exponential function to describe the instantaneous decay rate, k (Olsen, 1963), has come under criticism (MINDERMAN, 1968 ; ANDERSON, 1973a). This mathematical model implies that decomposition can be represented logarithmically, i.e., k is constant over the course of decomposition. This does not agree with the findings from field decomposition studies which indicate two exponential curves. The first curve defines a period of rapid initial weight loss brought about through the leaching and microbial exploitation of the chemically mobile fraction of the litter. The second curve describes the period of slower loss of material more resistant to decay (e.g., ligno-cellulose structural component of the litter). For *P. tremuloides* and *P. balsamifera* the period of rapid initial weight loss appears to be 8-12 months, i.e., before the subsequent litter fall of the succeeding year, the 'soluble' fraction disappearing during this period appears to be approximately 22 % dry weight for *P. tremuloides* and approximately 18 % for *P. balsamifera.*

It is evident that in any detailed study of litter decomposition litter in litter bags should be sampled as frequently as is practical during the first year in order to effectively monitor this critical phase of decomposition. After the initial rapid dry weight loss period, k will decrease much less rapidly per year and the logarithmic representation will be more realistic.
As in most published work on litter decomposition, litter bags were used in the present study. However, ANDERSON (1973a) has clearly outlined the hazards in the use of this method. In the course of the present investigation similar data to those presented by ANDERSON (1973a) have been obtained, i.e., for leaf litter of *P. balsamifera* decomposition rates were studied using 3 mm mesh and 10 mm mesh bags and also using tethered leaves and the following data were obtained at the end of one year : percent dry weight loss of litter in 3 mm mesh bags was 21.2, that in 10 mm mesh bags was 20.2, whilst that of tethered leaves was 38.1. Even after two years there had been only 28.2 % dry weight loss of litter held in 10 mm mesh bags. No similar study was attempted with leaves of *P. tremuloides* because they were not robust enough for tethering. As can be seen from the foregoing data, tethered leaves decompose significantly faster than those held in mesh bags. Litter held in bags probably represents a more uniform environment than is found in nature, i.e., the leaf material under study is not mixed with the litter of other, perhaps more nutrient rich and decomposable,

substrates ; whereas tethered leaves reflect a more natural mode of imposing test material into the litter or soil.

Litter bags themselves are frequently tied to stakes in the field, and this itself may lead to further difficulties particularly in long-term studies. If the bags are tied too tightly to stakes, then over a period of years the bags sink unevenly into the organic horizon and eventually contain leaves in various stages of decomposition (a fact which has been amplified by fungal isolation data from leaves held in litter bags for 3, 4 and 5 years - VISSER, unpublished data).

Despite these dangers, it is difficult to see how the use of litter bags can be avoided. The use of tethered leaves or large mesh bags is valuable if one is dealing with robust plant material and the investigation is only of short duration. However, in long-term studies the dangers of loss of comminuted material from tethered leaves or from those held in large mesh bags will be high.

The significance of the nutrient change data (Tables 3 and 4) is difficult to determine because analyses of the effects of leaching are not yet complete. For example, leaching-in and leaching-out rates of calcium have to be considered when determining whether this nutrient is being accumulated by biological activity. However, some preliminary general observations may be made.

CURLIN (1970) ranked $K > Ca > N > P$ in terms of susceptibility of these elements to leaching, and it appears in the system under investigation here that the nutrients can be ranked $K > Ca > Mg > N > P$. The rate of nutrient release, however, is somewhat different, with Curlin (1970) giving the rank $K > P > Ca \simeq N$. (calcium and nitrogen are released slowly because of the persistence of calcium as oxalate or carbonate and of nitrogen as insoluble protein or other organic complexes.

Data have been obtained (e.g., STARK, 1972 ; TODD et al., 1973) demonstrating the concentration of various elements by fungi, e.g., micro-fungal hyphae (Ca, K), Basidiomycete mycelium (Mg), rhizomorphs (Ca, K, Mg), basidiocarps (K, P). Calcium, magnesium, potassium and phosphorus are important in the nutrition of soil animals, and the fungi represent an important transfer link in the food web for such organisms as the fungivorous invertebrates, which lack some of the enzymes necessary for the breakdown of plant material.

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V. REFERENCES

ANDERSON, J.M. (1973a) – The breakdown and decomposition of sweet chestnut (*Castanea sativa* Mill.) and beech (*Fagus sylvatica* L.) leaf litter in two deciduous woodland soils. I. Breakdown, leaching and decomposition. Oecologia **12** : 251-274.

ANDERSON, J.M. (1973b) – The breakdown and decomposition of sweet chestnut (*Castanea sativa* Mill.) and beech (*Fagus sylvatica* L.) leaf litter in two deciduous woodland soils. II. Changes in the carbon, hydrogen, nitrogen and polyphenol content. Oecologia **12** : 275-288.

AUSMUS, B.S. and WITKAMP, M. (1974) – Litter and soil microbial dynamics in a deciduous forest stand. EDFB-IBP-73-10, Oak Ridge Nat. Lab., 183 p.

BRAY, J.R. and GORHAM, E. (1964) – Litter production in forests of the world. Adv. Ecol. Res. **2** : 101-157.

CARTER A. and LOUSIER, J.D. (1973) – Aspects of the radioecology of certain soil invertebrates in an aspen woodland ecosystem. Proc. 3rd Soil Microcom. Conf., SUNY, Syracuse, New York, 14 p.

Van CLEVE, K. (1971) – Energy - and weight - loss functions for decomposing foliage in birch and aspen forests in interior Alaska. Ecology **52** (4) : 720-723.

Van CLEVE, K. and SPRAGUE, D. (1971) – Respiration rates in the forest floor of birch and aspen stands in interior Alaska. Arctic and Alpine Res. **3** (1) : 17-26.

CURLIN, J.W. (1970) – Nutrient cycling as a factor in site productivity and forest fertilization. In Tree Growth and Forest Soils, C.T. Youngberg and C.B. Davey (eds.), pp. 313-325, Oregon State Univ. Press, Corvallis.

DASH, M.C. (1970) – A taxonomic study of Enchytraeidae (Oligochaeta) from Rocky Mountain forest soils of the Kananaskis region of Alberta, Canada. Can. J. Zool. **48** : 1429-1435.

DASH, M.C. and CRAGG, J.B. (1972a) – Selection of microfungi by Enchytraeidae (Oligochaeta) and other members of the soil fauna. Pedobiologia **12** : 282-286.

DASH, M.C. and CRAGG, J.B. (1972b) – Ecology of Enchytraeidae (Oligochaeta) in Canadian Rocky Mountain soils. Pedobiologia **12** : 323-335.

GOSZ, J.R., LIKENS, G.E. and BORMANN, F.H. (1973) – Nutrient release from decomposing leaf and branch litter in the Hubbard Brook Forest, New Hampshire. Ecol. Monogr. **43** : 173-191.

KIRA, T. and SHIDEI T. (1967) – Primary production and turnover of organic matter in different forest ecosystems of the western Pacific. Jap. J. Ecol. **17** (2) : 70-87.

KIRBY, C.L. (1973) – The Kananaskis Forest Experiment Station, Alberta (History, Physical Features and Forest Inventory). Inf. Rep. NOR-X-51, N.F.R.C., C.F.S., Environment Canada, Edmonton, Alberta. 50 p.

LEMEE, G. and BICHAUT, N. (1973) – Recherches sur les écosystèmes des réserves biologiques de la forêt de Fontainebleau. II. Décomposition de la litière de feuilles des arbres et libération des bioéléments. Oecol. Plant. **8** (2) : 153-174.

LOUSIER, J.D. (1974) – Effects of experimental soil moisture fluctuations on turnover rates of Testacea. Soil Biol. Biochem. **6** : 19-26.

MINDERMAN, G. (1968) – Addition, decomposition and accumulation of organic matter in forests. J. Ecol. **56** : 355-362.

MITCHELL, M.J. (1973) – An improved method for microrespirometry using gas chromatography. Soil. Biol. Biochem. **5** : 271-274.

MITCHELL, M.J. (1974) – Ecology of Oribatid mites (Acari : Cryptostigmata) in an aspen woodland soil. Ph.D. Thesis, Dept. of Biology, University of Calgary, Canada. 220 p.

NEWBOLD, P.J. (1967) – Methods for estimating the primary production of forests. IBP Handbook 2, Blackwell's, Oxford.

OLSEN, J.S. (1963) – Energy storage and the balance of producers and decomposers in ecological systems. Ecology **44** (2) : 322-331.

PARKINSON, D. (1971) – Studies on fungi in Canadian aspen forest soils. In Productivity of Forest Ecosystems, Proc. Brussels Symp., 1969, pp. 425-430, UNESCO.

PETERSON, E.B., CHAN, Y.H. and CRAGG, J.B. (1970) – Above ground standing crop, leaf area and caloric value in an aspen clone near Calgary, Alberta. Can. J. Bot. **48** : 1459-1469.

RAPP, M. (1971) – Cycle de la matière organique et des éléments minéraux dans quelques écosystèmes méditerranéens. Progr. biol. internat., Ecol. du Sol, C.N.R.S., Paris, 23-184.

STARK, N. (1972) – Nutrient cycling pathways and litter fungi. Bioscience **22** : 355-360.

TODD, R.L., CROMACK, K. and STORMER, Jr., J.C. (1973) – Chemical exploration of the microhabitat by electron probe microanalysis of decomposer organisms. Nature **243** : 544-546.

Table 1. Summary of above-ground litter input and biocontent data for the aspen woodland.

	Litter input (g.d.wt. m^{-2})	Caloric input (kcal m^{-2})	Carbon input (g m^{-2})
Trees			
Leaf litter	250 Aspen : 215 Balsam : 35	1,180 **	121
Non-leaf litter	70 *	330	34
Understory	150	705 **	70
Total	470	2,215	225

* 70 g m^{-2} represents an estimate of 21 % of total litter input (BRAY and GORHAM, 1964). Because the aspen woodland is a successional forest the ratio non-leaf litter : leaf litter may approach the ratios given by KIRA and SHIDEI (1967), i.e., 1:2 to 1:1;

** 4.72 kcal g^{-1} used for aspen leaf litter (PETERSON et al., 1970)
4.70 kcal g^{-1} used for understory litter (NEWBOLD, 1967)

Table 2. Percentage dry weight loss and rate of loss, k, for aspen woodland leaf litter.

Time (months after burial)	*Populus tremuloides*		*Populus balsamifera*	
	% dry wt. loss	k	% dry wt. loss	k
1	2.86 ± 0.35	0.307	2.00 ± 0.26	0.240
5	18.34 ± 0.70	0.486	15.34 ± 0.70	0.400
8	23.32 ± 1.74	0.401	19.27 ± 0.93	0.339
12	26.16 ± 0.60	0.303	21.16 ± 0.28	0.283
18	34.66 ± 0.86	0.264	27.55 ± 0.68	0.213

Table 3. Concentrations (in %) of carbon, hydrogen and nitrogen in aspen and balsam poplar leaves after various periods of decomposition.

Time (months after burial)	*Populus tremuloides*				*Populus balsamifera*			
	C	H	N	C/N	C	H	N	C/N
0	49.12	6.11	1.08	45.48	51.27	5.69	1.03	49.78
1	48.54	6.03	1.08	44.94	51.27	5.58	1.10	46.61
5	49.18	5.38	1.40	35.13	51.92	5.76	1.47	35.32
8	50.24	5.65	1.69	29.72	51.53	5.43	1.54	33.46
12	49.29	5.45	1.62	30.43	51.92	5.38	1.84	28.22

Table 4. Concentrations (in mg nutrient per g leaf tissue remaining) of nutrients in aspen and balsam poplar leaves after various periods of decomposition.

Time (months after burial)	*Populus tremuloides*				*Populus balsamifera*			
	Ca	Mg	K	P	Ca	Mg	K	P
0	22	2.5	7.1	2.1	24	2.6	13.2	2.2
1	23	2.5	7.0	2.0	23	2.7	9.9	2.2
5	27	2.8	5.1	1.4	29	3.5	6.0	2.4
8	31	2.7	3.2	2.0	29	3.2	3.9	2.1
12	32	2.8	4.1	1.7	33	3.3	4.6	1.9

Table 5. Comparison of k values for a range of deciduous litter (in some cases these have been calculated from the literature data).

Site	Tree Species	k	0.693/k (yrs)	Reference
Blean Woods, England	*Castanea sativa*	0.406-0.623	1.1-1.7	Anderson, 1973
	Fagus sylvatica	0.218-0.327	2.1-3.2	Anderson, 1973
Fontainebleau	*Fagus sylvatica*	0.520-0.230	1.3-3.0	Lemée & Bichaut, 1973
	Quercus petraea	0.533	1.3	Lemée & Bichaut, 1973
	Carpinus betulus	0.910	0.8	Lemée & Bichaut, 1973
Alaska	*Betula papyrifera*	0.456	1.5	van Cleve, 1971
	Populus tremuloides	0.389	1.8	van Cleve, 1971
	Alnus crispa ssp. *sinuata*			
	Hulk in *B. papyrifera*	0.408	1.7	van Cleve, 1971
	Hulk in *P. tremuloides*	0.423	1.6	van Cleve, 1971
Hubbard Brook, New Hampshire	*Acer saccharum*	0.510	1.4	Gosz, Likens and Bormann, 1973
	Fagus grandifolia	0.370	1.9	Gosz, Likens and Bormann, 1973
	Betula allegheniensis	0.850	0.8	Gosz, Likens and Bormann, 1973
Oak Ridge, Tennessee	*Liriodendron tulipifera*	0.852	0.8	Ausmus & Witkamp, 1974
	Fraxinus pennsylvanica	0.768	0.9	Ausmus & Witkamp, 1974
	Carya tomentosa	0.788	0.88	Ausmus & Witkamp, 1974
	Quercus spp.	0.707	0.98	Ausmus & Witkamp, 1974
	Acer rubum	0.883	0.78	Ausmus & Witkamp, 1974
	Cornus florida	1.152	0.6	Ausmus & Witkamp, 1974
Kananaskis	*Populus tremuloides*	0.264	2.4	
	Populus balsamifera	0.213	3.3	

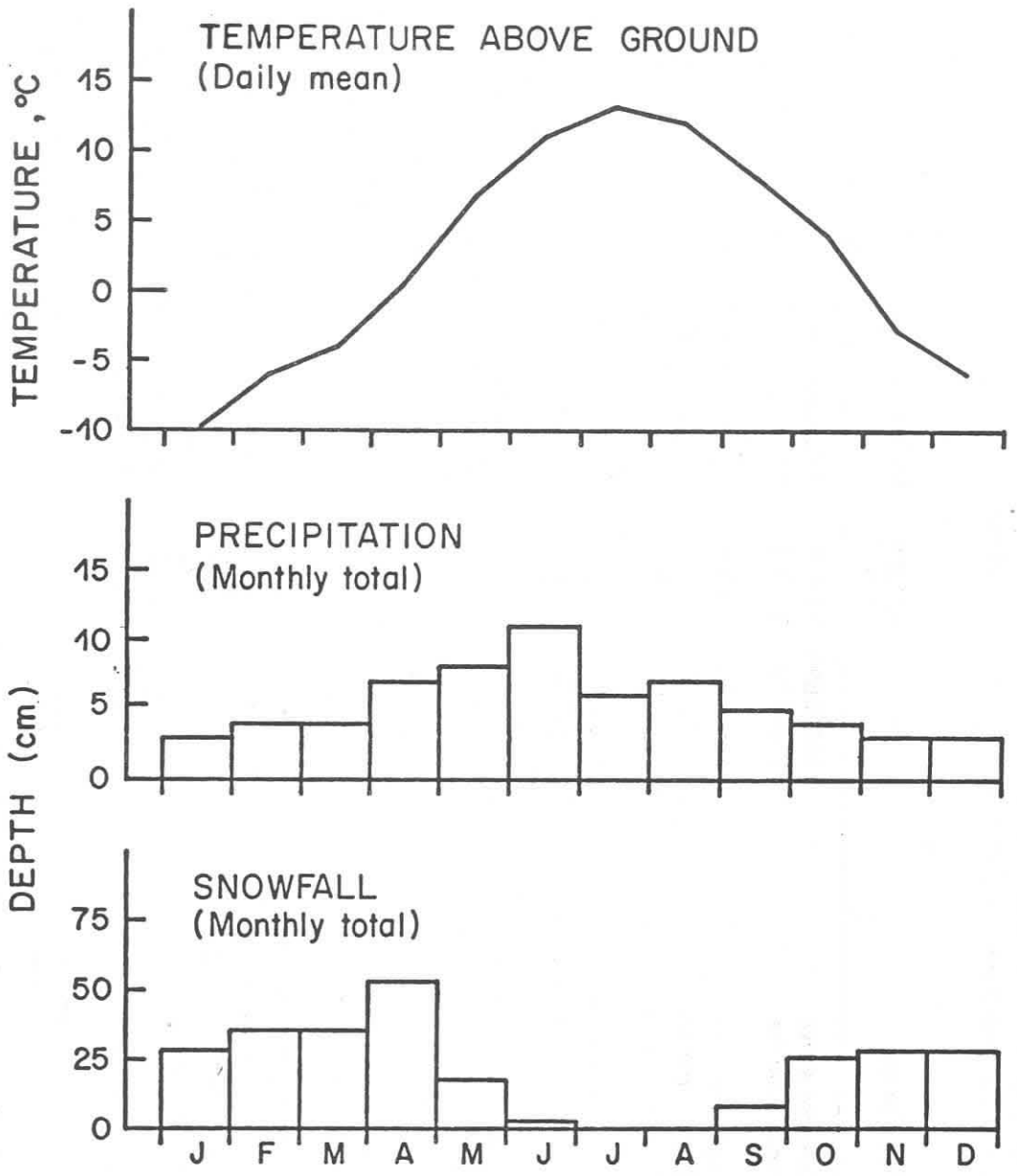

Figure 1. Summarized climatic data (1939-1970) for experimental area (adapted from KIRBY, 1973).

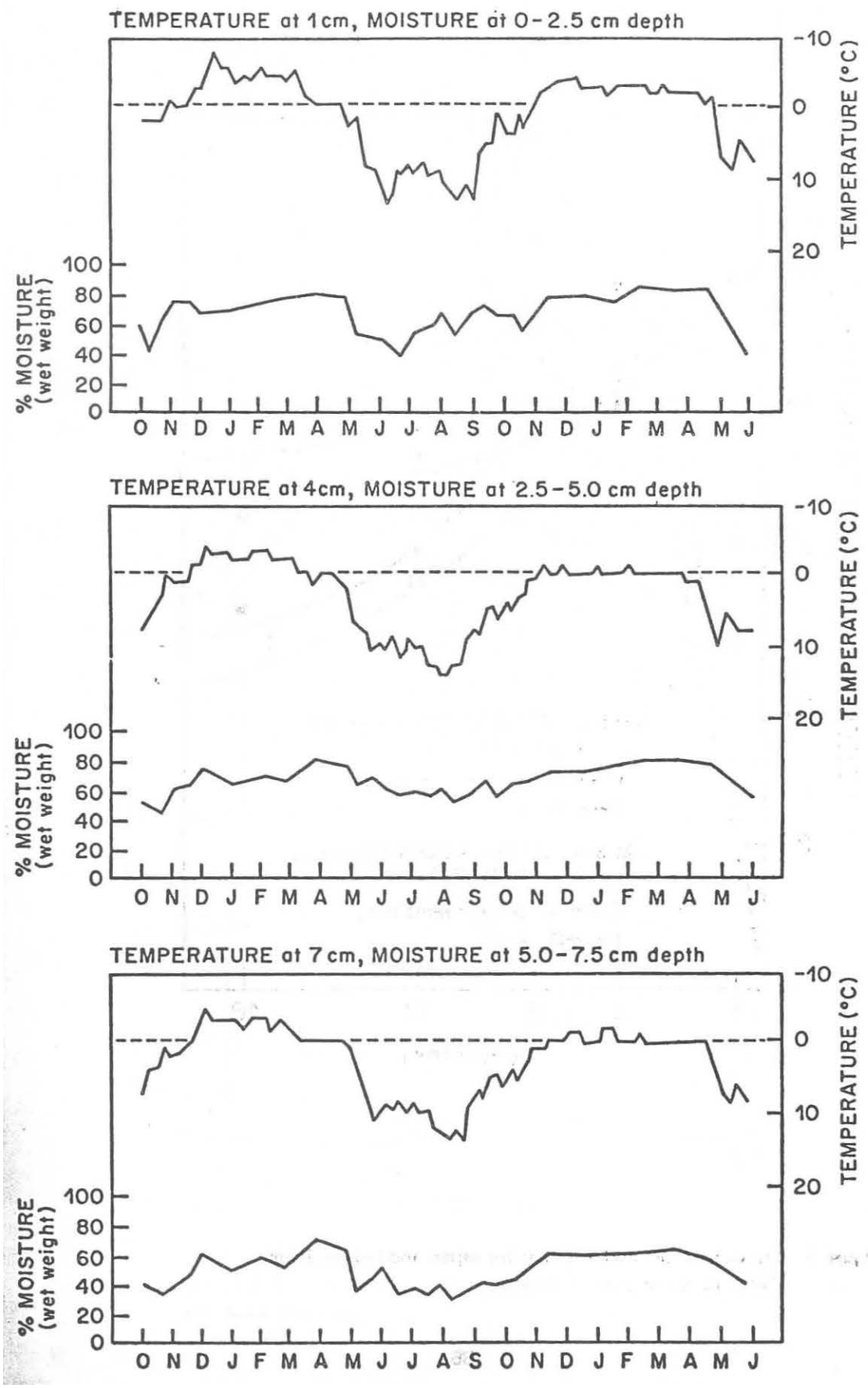

Figure. 2 Litter temperature and moisture conditions at three depths in the aspen site (Oct. 1971 - June 1973). (adapted from MITCHELL, 1974)

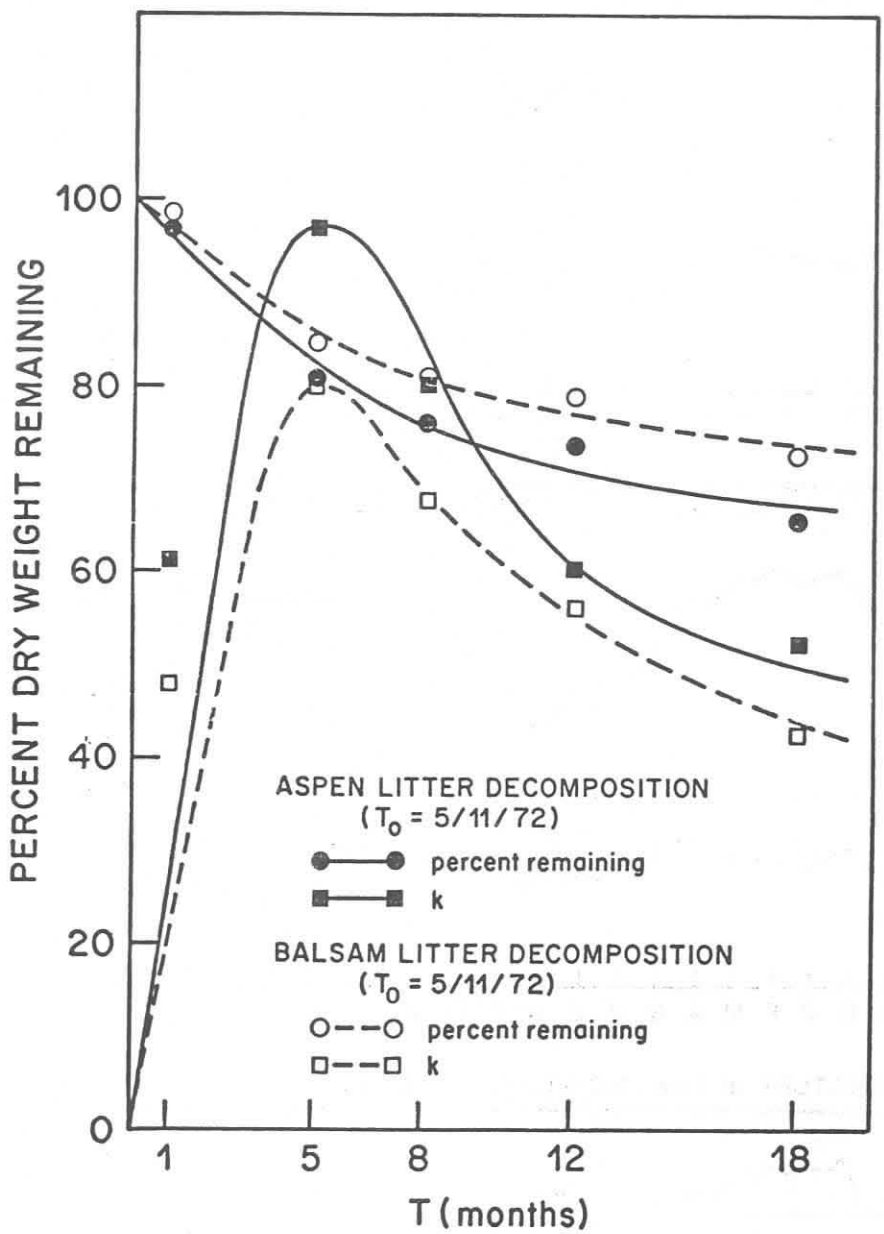

Figure 3. Dry weight loss and K values for aspen and balsam litter. Values of K are given in table 2.

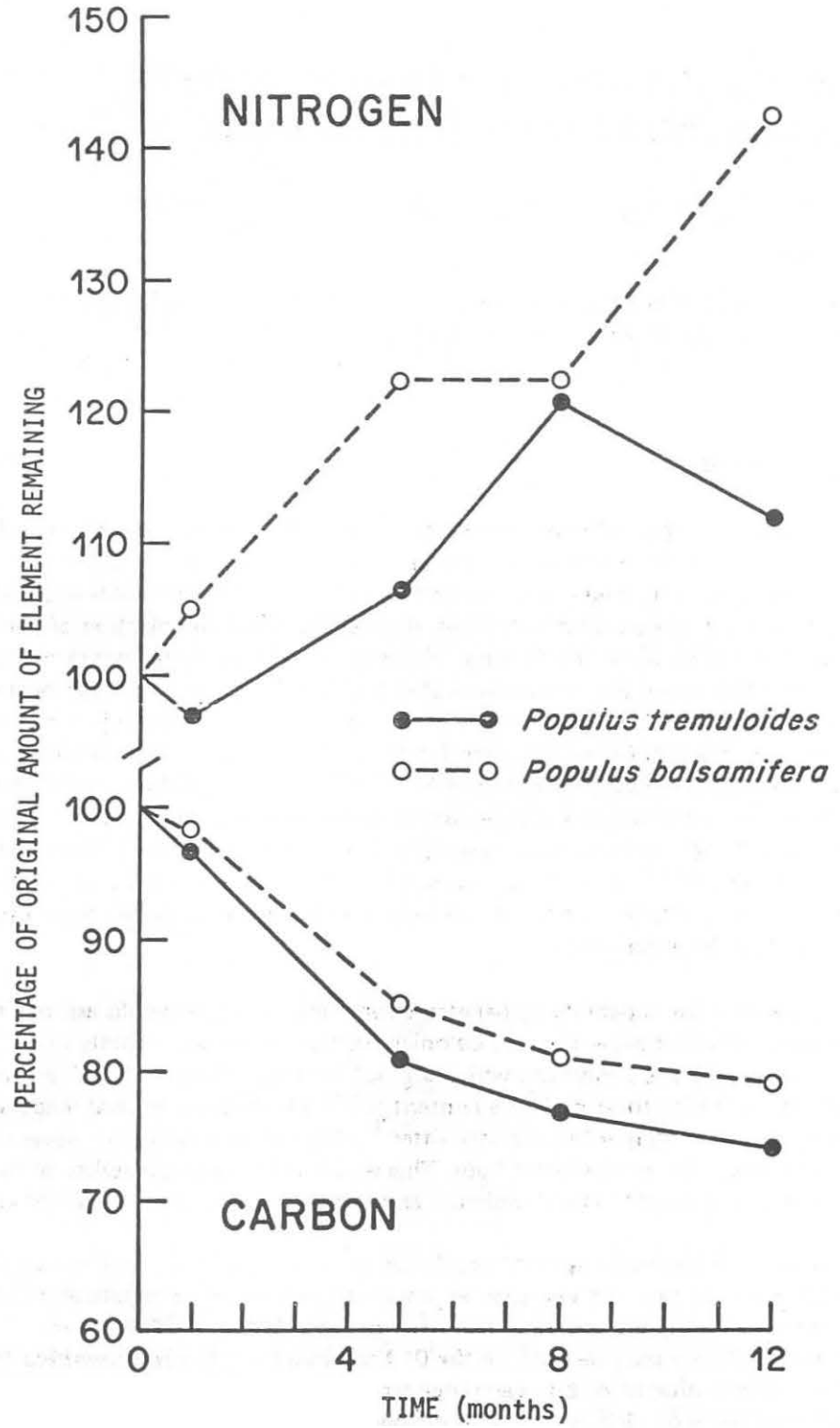

Figure 4. Amounths of carbon and nitrogen in leaf litter at various early stages of decomposition.